

second type of social calls were also recorded when a *P. pipistrellus* passed the Lesser noctules. At the same time sequences of short pulses (3–4 ms, probably multiharmonic) with end frequencies of about 10 kHz (interpulse duration ca. 6 ms) were recorded. Figure 11 shows part of such a sequence enclosing an echolocation pulse.

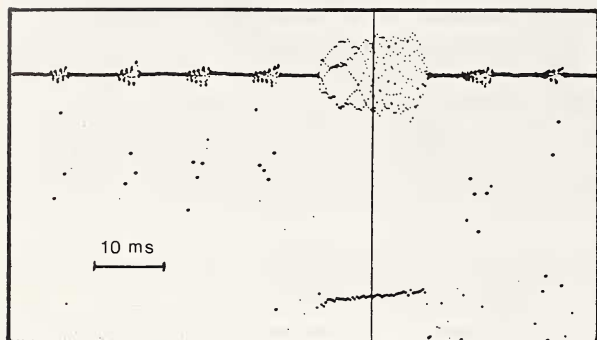


Fig. 11. *Nyctalus leisleri*. Oscillogram and superimposed period plot showing a search pulse ($T=14.9$ ms, $f_s=28.0$ kHz, $f_c=24.8$ kHz, $f_{max}=f_e=24.0$ kHz) and part of a sequence of ten short pulses of social context ($T=2.7$ – 4.2 ms, f_e ca. 10 kHz, interpulse duration = 4.6–8 ms). The vertical cursor indicates the pulse center of the search pulse. The total time from the start of the first short pulse to the end of the tenth short pulse was 113 ms

In southern Switzerland the social calls resembling type 1 and 2 of Meiringen were recorded during the mating season (August 86) and there was no indication that interactions with other species occurred. On the basis of the similar structure and the combined occurrence of call type 1 and 2 at Meiringen as well as in Southern Switzerland, I assume that these two types of social calls were actually emitted by individuals of *Nyctalus leisleri* at both recording sites.

In the field, the social call of type 2 could be confused with echolocation pulses of *Tadarida teniotis* (ZBINDEN and ZINGG 1986). But signal analysis shows that search calls of *T. teniotis* have not such a high start frequency and are not normally of linear period modulation.

Acknowledgements

I wish to thank ELISABETH BUCHER and RAPHAËL ARLETTAZ for their precious help in the fieldwork. Prof. V. AELLEN kindly supplied me with Russian literature, parts of which were translated by Mrs. V. SCHNELL and R. HODEL. I thank Dr. O. BERNATH, Departement of Audiology of the Berne University Hospital, for permitting the use of the FFT-analyser. I am greatly indebted to Dr. KARL ZBINDEN for critically reading the manuscript, making important suggestions for its improvement and correcting the text. This study was supported by the Swiss National Science Foundation (grant no. 3.177-0.85).

Zusammenfassung

Suchflugortungslaute von Nyctalus leisleri und Pipistrellus savii (Mammalia: Chiroptera) in der Schweiz

Suchflugortungslaute jagender *Nyctalus leisleri* und *Pipistrellus savii* wurden mittels QMC S100 Detektor und 8:1 Frequenzteiler auf der schweizerischen Alpennord- und Alpensüdseite registriert. Bei beiden Arten wurden sowohl schwach frequenzmodulierte als auch konstantfrequente Suchfluglaute festgestellt.

Für 204 analysierte Suchfluglaute von *N. leisleri* waren folgende Medianwerte charakteristisch: Signaldauer 9.2 ms, Anfangsfrequenz 25.1 kHz, Zentrumsfrequenz 24.3 kHz, Endfrequenz 23.7 kHz, Signal-Bandbreite 1.6 kHz. Die Intervalldauer ($N=2153$) zwischen den Signalen zeigte eine bimodale Verteilung, mit einem starken Modus bei 243 ms und einem zweiten, schwächeren bei 350 ms.

Für 236 Suchfluglaute von *P. savii* waren folgende Medianwerte typisch: Signaldauer 12.1 ms, Anfangsfrequenz 34.2 kHz, Zentrumsfrequenz 32.8 kHz, Endfrequenz 32.0 kHz, Signal-Bandbreite 2.2 kHz. Die Intervalldauer ($N=1341$) zwischen den Signalen war bimodal verteilt, mit einem starken Modus bei 192 ms und einem zweiten, schwächeren bei 294 ms. Bei beiden Spezies wurden zwischen verschiedenen Variablen der Suchfluglaute signifikante Korrelationen ermittelt.

Zusätzlich werden als Soziallaute interpretierte Ruftypen von *N. leisleri* beschrieben. Der erste Typ bestand aus einer Gruppe von vier Lauten im Frequenzbereich von 38–16 kHz. Der zweite Typ, ein linear periodenmodulierter Einzellaut ($T=20\text{--}27$ ms), überstreicht ein Frequenzband von 21–10 kHz und kann im Felde mit Ortungsrufen von *Tadarida teniotis* verwechselt werden.

References

- AHLEN, I. (1981): Identification of Scandinavian Bats by their sounds. Swed. Univ. of Agricult. Sci. Dept. Wildlife Ecol., Report 6, Uppsala.
- FENTON, M. B.; BELL, G. P. (1981): Recognition of Species of Insectivorous Bats by their Echolocation Calls. *J. Mammalogy* **62**, 233–243.
- HARTLEY, D. J. (1985): Analysis of the echolocation behaviour of some British bats recorded in the field. Ph. D. Thesis, Polytechnic of Central London. Queen Mary Coll., Univ. London.
- HOOPER, J. H. D. (1969): Potential use of a portable ultrasonic receiver for the field identification of flying bats. *Ultrasonics* **7**, 177–181.
- HORACEK, I.; HANAK, V. (1986): Generic status of *Pipistrellus savii* and comments on classification of the genus *Pipistrellus* (Chiroptera, Vespertilionidae). *Myotis* **23–24**, 9–16.
- KONSTANTINOV, A. I.; MAKAROV, A. K. (1973): Echolocating signals of some native species of bats (Vespertilionidae). In: Problems of comparative physiology of analysers. Vol 3: Echolocation in bats. Ed. by E. Sh. Airapetianz. Leningrad: Publishing House of the State Leningrad University. 29–44. (In Russian).
- MILLER, G. S. (1912): Catalogue of the Mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. London: British Museum (N.H.).
- MILLER, L. A.; DEGN, H. J. (1981): The Acoustic Behavior of Four Species of Vespertilionid Bats Studied in the Field. *J. Comp. Physiol. A* **142**, 67–74.
- PATLJAKEVITSCH, N. D. (1980): Echolocation signals of Vespertilionidae. In: Rukokrylyje (Chiroptera). Ed. by V. E. Sokolov. Moscow: Nauka. 213–270. (In Russian).
- PYE, J. D. (1978): Some preliminary observations on flexible echolocation systems. In: Proc. Fourth Internat. Bat Research Conf. Ed. by R. J. Olembo, J. B. Castolino and F. A. Mutere. Nairobi: Kenya Literature Bureau. 127–136.
- PYE, J. D. (1980): Adaptiveness of echolocation signals in bats. Flexibility in behaviour and in evolution. *Trends in NeuroSciences (TINS)*, October 1980, 232–235.
- SACHS, L. (1978): *Angewandte Statistik*. Berlin, Heidelberg, New York: Springer-Verlag.
- TUPINIER, Y.; BIRAUD, Y.; CHIOLLAZ, M.; ESCUDIE, B. (1980): Analysis of vespertilionid sonar signals during cruise, pursuit, and prey capture. In: Proceedings of the Fifth International Bat Research Conference. Ed. by D. E. Wilson and A. L. Gardner. Lubbock (Texas): Texas Tech. Univ. Press. 29–38.
- VOGLER, B.; NEUWEILER, G. (1983): Echolocation in the noctule (*Nyctalus noctula*) and horseshoe bat (*Rhinolophus ferrumequinum*). *J. Comp. Physiol. A* **152**, 421–432.
- WATSON, A. (1970): Electronic aids to the identification of bats in flight and to their study under natural conditions. *Bijdragen tot de Dierkunde* **40**, 99–102.
- ZBINDEN, K.; ZINGG, P. E. (1986): Search and hunting signals of echolocating European free-tailed bats, *Tadarida teniotis*, in southern Switzerland. *Mammalia* **50**, 9–25.

Author's address: PETER E. ZINGG, Institute of Zoology, University of Berne, Baltzerstrasse 3, CH-3012 Berne, Switzerland

The development of visual acuity in treeshrews (*Tupaia belangeri*)

By BIRGIT HERTENSTEIN, ELKE ZIMMERMANN and H. RAHMANN

Institute of Zoology, University Hohenheim, Stuttgart

Receipt of Ms. 1. 6. 1987

Abstract

Ontogenetic development of visual acuity was tested in 14 young treeshrews (*Tupaia belangeri*) from the moment of eye opening (day 16 to 23) until leaving their nest (day 30 to 34), using an optomotoric drum. First optokinetic nystagmus (OKN) was found between day 4 and 5 after eye opening with individual values of visual acuity varying considerably between 34,5 and 370 minutes of arc. Before leaving the nest all values were about 11 minutes. In general, the longer the process of eye opening took (from a few hours to three days) the later was the first OKN. No correlation was found between the onset of eye opening and the first OKN. There were no differences in the development of visual acuity between the two sexes. In addition to the optomotoric drum training, visual acuity of two adult male tupaia was determined using a visual discrimination choice apparatus. According to all tests, visual acuity of adult treeshrews was found to be 10 and 8,6 minutes respectively. The extent of visual acuity found in this study was compared with that of some primates.

Introduction

Currently the Tupaiidae are considered to be the group of recent mammals that is most similar to the ancestors of primates (STARCK 1978). However, despite numerous morphological, physiological and ethological investigations, there has been no final decision as to their relationship to other mammalian taxa (LUCKETT 1980). Therefore, they have been placed in a separate mammalian order, Scandentia. The diurnal and semiarboreal tupaia live in southeast Asia, where males occupy overlapping home ranges with females (KAWAMICHI and KAWAMICHI 1979). They feed on different sorts of fruit, insects and even some smaller vertebrates. Their senses of smell and hearing as well as their vision are highly developed.

Visual acuity of adult tupaia has already been determined with visual discrimination training but with different results. Thus, ORDY and SAMORAJSKI (1968) have found a visual angle of 0,5 to 1,5 min of arc and SCHÄFER (1969) has reported one of 6,8 min of arc. Even though research on the visual acuity of the eye in various groups of animals has been reported in the past and with many different methods (RAHMANN 1967; BOOTHE et al. 1985; for review), so far there is no information on the ontogenetic development of vision in *Tupaia belangeri*.

The purpose of this study is to show how visual acuity develops in young tupaia from the moment of eye opening until after they leave their nests, and thus, to provide a basis for comparison with the visual development of various primates.

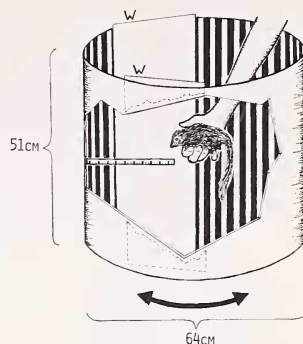
Material and methods

Determination of visual acuity during development of tupaia by means of the optomotoric nystagmus (OKN)

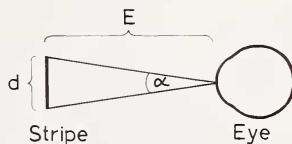
14 young tupaia born at the breeding colony at the Department of Zoology, University of Stuttgart Hohenheim, were tested. Housing and maintenance of breeding pairs and postnatal behavioral development of young has been described previously (HERTENSTEIN et al. 1987). Tupaia are born

blind. Data collection began at eye opening about 19 days after birth, and continued another 10 to 12 days until they had left their nest box for the first time. At this time tupaia develop a highly coordinated locomotor ability to move through their semi-arboreal environment and react promptly to potential dangers.

Fig. 1. Optomotoric drum for determination of visual acuity of young treeshrews. (w = white sheet, used to reduce the visual field of the animal)



The experiments were conducted in an optomotoric drum having a height of 51 cm and a diameter of 64 cm, with vertical black and white stripes of equal width (Fig. 1). There were 15 different stripe-patterns each of them having a particular width of stripes ranging from 12 mm to 0.4 mm. A 75W bulb, hanging over the centre of the barrel, provided equal illumination. There were no windows or other light in the room. The animals were found to remain calm if held by hand while being tested. Visual acuity was tested once each day in the morning. The young were taken out of the parental cage within their nestboxes. The animals were allowed to adapt to the light for 15 to 20 min. Testing started with the pattern with the widest stripes ($d = 12$ mm) in a short distance ($E = 10$ cm, see Fig. 2). The distance E was increased, if the animal showed a clear optomotoric nystagmus (OKN). The next smaller stripe pattern was used once the distance between head and pattern could not be increased any further (diameter of the barrel = 32 cm). Visual acuity was calculated from the exact field of sight (E) at which, for a definite width of stripes (d), the animals still responded with an OKN, using the formula in Fig. 2.



$$\text{VISUAL ANGLE } \alpha = \frac{d [\text{cm}] \cdot 180^\circ}{\pi \cdot E [\text{cm}]} \left[\begin{array}{l} \text{degrees} \\ \text{of arc} \end{array} \right]$$

Fig. 2. Formula for calculating visual acuity. (See text for details)

As the attention of the animals decreased rapidly, they tried to leave the hand or simply went to sleep. Therefore many rests were necessary during each experiment and in some cases the test had to be broken off completely.

Determination of visual acuity in adult tupaia by means of visual discrimination tests

The tests in this case were run with two adult male tupaia of an age of 4½ and 7½ months respectively, both of which had been reared by hand (HERTENSTEIN et al. 1987). The animals were kept individually in wooden cages of a size of 0.5 m³, and containing branches for climbing, shelves for sitting upon and a sleeping box. The ground was covered by fine sawdust and straw. Their food consisted of tupaia-pellets (by Altromin) and water ad lib., in addition to fruit, sunflower seeds, nuts, oatmeal, egg and cat food given in rotation. Insects were not used in the diet, since mealworms (*Tenebrio larva*) were used as rewards in the discrimination tests.

The "two alternative discrimination apparatus" utilized was similar to training systems used to test visual acuity in golden hamsters (*Mesocricetus auratus*), lemmings (*Lemmus lemmus*, *Myopus schisticolor*) and various species of american deermice (*Peromyscus*) (RAHMANN 1961; RAHMANN and ESSER 1965; RAHMANN and RAHMANN 1966; RAHMANN et al. 1968). From a start box (Fig. 3) the animals enter the choice box where they have to decide between one of two patterned doors at the end of the choice box, separated by a partition. The patterns for the discrimination experiments were fixed to the doors. The patterns could be changed quickly from one side to the other by pulling strings. If the animal chose the correct door, he received a piece of mealworm as a reward. The animals made their

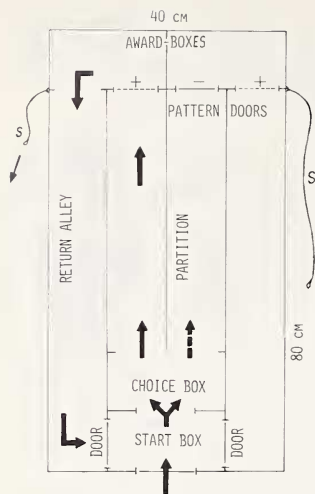


Fig. 3. Discrimination apparatus for determination of visual acuity of adult treeshrews. Pattern doors were manually alternated from left to right by pulling strings (s)

way back to the start box through return alleys, and the next test was started immediately. The whole apparatus was covered by a lid of plexiglas with slots for ventilation and presentation of rewards. A 75W bulb was hung just above the apparatus to illuminate the area around the patterned doors.

The tests were run once a day in the morning. The animals had to decide between a pattern of black and white vertical stripes of equal width (positive pattern, with reward) and a grey surface of the same brightness (negative pattern, door locked). The pattern was offered both on the right and on the left door, 20 times each, in a predetermined, irregular order. There were 14 different patterns with various widths of stripes from 12 mm to 0.6 mm. The distance between the choice box and the pattern doors was 48 cm. The criterion of significance for the number of correct choices in 40 runs was fixed at 70 %, for a 99 % probability (KOLLER 1969). If the results of a test were not significant after an obvious lack of concentration of the test animal, the test was repeated with the same width of stripes on the following day. Quite often the result was then significant. To avoid the possibility that the animals were choosing different degrees of brightness of the patterns rather than deciding between stripe pattern and plain grey, a second series of tests was run, in which a choice had to be made between a vertical stripe pattern (positive pattern) and a horizontal one. All the other conditions of the test remained the same. Subsequently visual acuity was determined for a shorter choice distance of 27 cm, in order to have a comparison between greater and shorter choice distances.

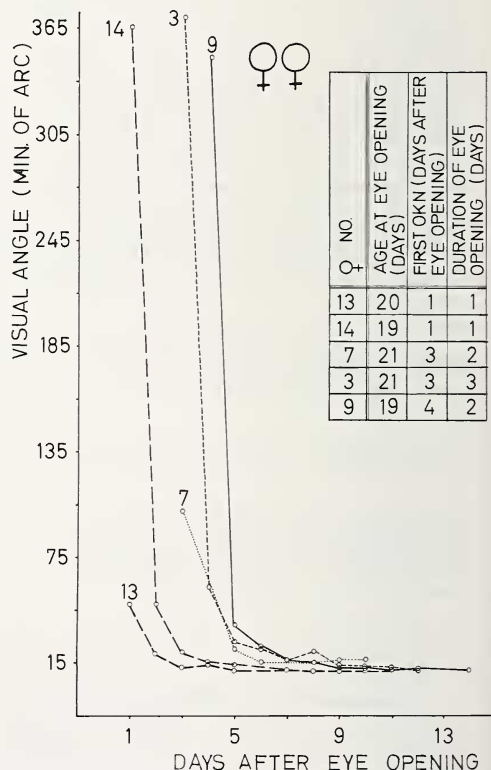
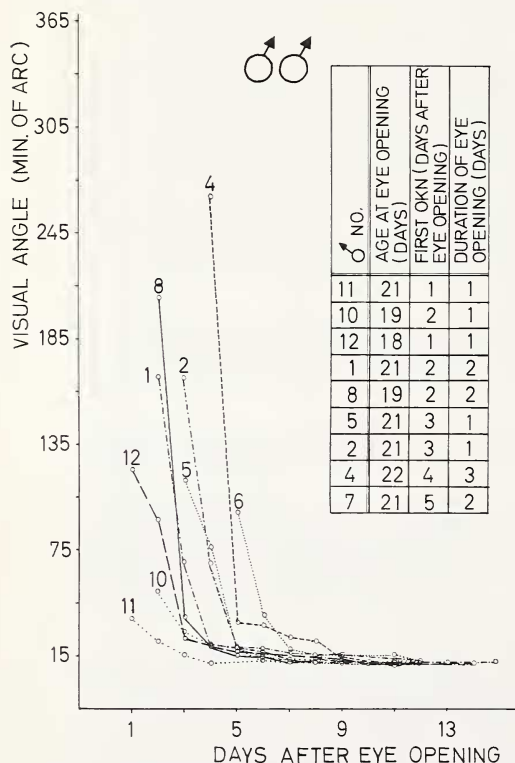


Fig. 4. Development of visual acuity in 9 male and 5 female treeshrews. (For youngsters from the same litter identical symbols are used)

Results

Development of visual acuity during development of *Tupaia belangeri*

As shown in fig. 4a and b, four animals responded with a clear optomotoric reaction on the first day after eye opening. A first reaction was shown by three animals on the second day after eye opening, three on the third day, two on the fourth and one on the fifth. Within this period the individual visual angle varied considerably ($34,5 \text{ min}$ to $370 \text{ min} = 6,2^\circ$). During the following eight days the range of the values decreased and, by the time the animals left their nests, they had reached a similar level of $11 \pm 0,75$ minutes in the males and of $11,7 \pm 2,68$ minutes in the females. The great interindividual differences in the first occurrence of an OKN and the values for visual acuity might be caused not only by different visual efficiency, but also by the stress on particularly sensitive animals when being handled.

When their eyes started to open the test animals were between 18 and 22 days old. Separation of the eyelids took as long as three days but, in other cases, just a few hours. Notwithstanding how long the process of the eye opening took, the start of the process was counted as day number one. The first optomotoric response tended to be delayed when the process of eye opening took longer (see tables in Fig. 4a and b). No correlation between the age of the test animals at the start of the eye opening and the first OKN was found.

Visual acuity of adult tupaia

First, the animals were allowed to become familiar with the discrimination choice apparatus. They were rewarded if they used the striped door by chance (width of stripes in this case 12 mm). On the second test day test animal H (VT_H) already chose the striped door significantly more often than the plain grey door. Test animal W (VT_W), which was only $4\frac{1}{2}$ months old, seemed nervous during the daily 5 to 10 minutes in the apparatus and took 7 days before he chose significantly between the two alternatives. To determine visual acuity (minimum separable = perception of separation between stripes), the width of stripes was gradually reduced, from 7 to 0,6 mm, during the following days of testing, whereas the length of the partition was 48 cm. The door with the negative pattern remained locked. An attempt to go down the wrong alley for more than one head-length was scored at a miss. VT_H chose significantly between stripes and plain grey down to a width of stripes of 1,4 mm (see Fig. 5). This is equivalent to a visual angle of 10 minutes of arc. VT_W discriminated a stripe width of 12 mm, equivalent to a visual angle of 8,6 minutes of arc. Visual acuity for choosing between horizontal and vertical stripes was 11,5 minutes for VT_H and 10 for VT_W . This is virtually the same as was found in the first set of experiments. As the partition and thus the distance E was reduced from 48 to 27 cm VT_W did not show any change of efficiency in his visual acuity. For the stripe width of 0,8 mm, which VT_W could still discriminate, the visual angle was 10,2 minutes. VT_H , on the other hand, tended to choose one particular side increasingly as the experiment proceeded. This made a determination of the smallest visual angle impossible.

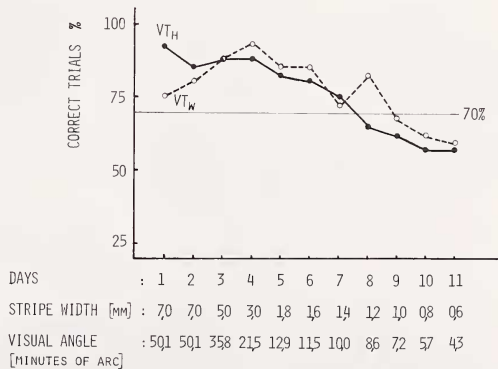


Fig. 5. Number of correct trials after the gradual reduction of the stripe width. (Day one means the first training day after learning the pattern discrimination)

There were great differences in how the animals behaved in the apparatus. Sometimes they were calm and attentive to the apparatus. In other instances, the test animal dashed around the apparatus in a hectic manner. An animal might rush into one of the choice alleys, realize his error, and then quickly turn around and go into the correct alley. A run of this sort was scored as a miss, even though after an initial error at the partition, the animal definitely made the right choice.

Discussion

Many physiological as well as psychological factors influence determination of visual acuity. Thus results of this study might not be directly comparable with the results of previous authors or investigations into other species. Methods of investigating visual acuity often vary considerably from author to author. Different intensities of illumination can produce differences in the results, as could be shown by CAVONTUS and ROBBINS (1973) with rhesus monkeys and RAHMANN et al. (1968) with deermice (*Peromyscus*). Moreover, the willingness and ability to concentrate shown by the test animals plays a role (RAHMANN 1967). Thus, the failure to perform, which occurred again and again in this study, both in the training apparatus and in the drum, might be the result of many factors including distraction, weariness, and stress of the test animals.

The value for visual acuity of 8,6 minutes of arc, which has been obtained with the adult tupaia in our training apparatus, is similar to the results of SCHÄFER (1969) found in a comparable discrimination apparatus for tupaia (visual acuity: 6,8 minutes of arc). Using a "noncorrection method of training", ORDY and SAMORAJSKI (1968) found a visual acuity of tupaia of 0,5 to 1,5 minutes of arc which appears quite high (Tab. 1).

Figure 6 shows the time course of the development of visual acuity in tupaia compared with that of some primates: tupaia and rhesus monkeys achieve some 14 minutes at an age of about one week after eye opening (rhesus and other primates: eyes are open at birth). Baboons show this value soon after birth (FOBES and KING 1982). Pig-tailed macaques (*Macaca nemestrina*) pass the limit of 14 minutes after 2 to 3 weeks, gibbons after 3 weeks, oranges after 5 weeks and man after about 11 weeks (FOBES and KING 1982). A bushbaby (*Galago senegalensis*; behaviourally investigated by ZIMMERMANN 1987) tested with the same method, showed a visual acuity of 18,7 minutes after 25 days (end of the experiment). Obviously with increasing phylogenetic level, the speed of development of visual acuity slows down. This is consistent with the observation that the "higher" the phylogenetic

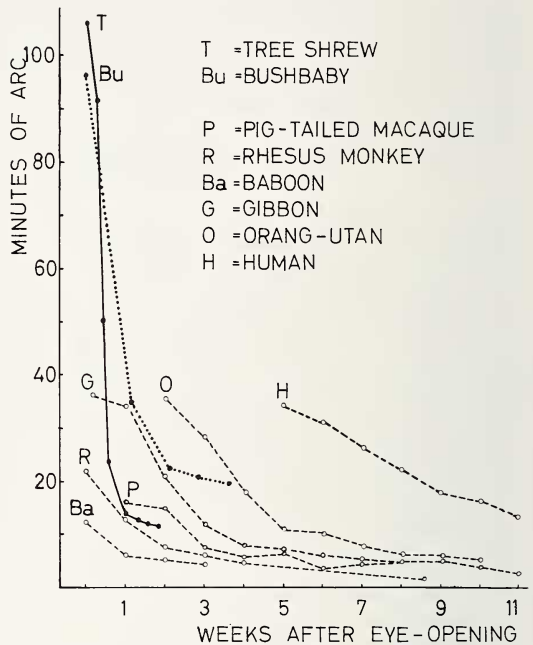


Fig. 6. Development of visual acuity in tupaia in comparison to that of some primates. (Treeshrews and bushbaby from own data, other data from FOBES and KING 1982)